Title: The phylogenetic position of the Yunxian cranium elucidates the origin of Dragon Man and the Denisovans

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Abstract: Diverse Middle Pleistocene forms of *Homo* coexisted in Africa, Europe, and Asia. It is very controversial whether these fossil humans represent different species or lineages. The ~1 Ma old Yunxian 2 fossil from China is crucial for understanding the cladogenesis of *Homo* and the origin of *Homo sapiens*. Here, we restored and reconstructed the distorted Yunxian 2 cranium using new technology. The results show that this cranium displays mosaic features of plesiomorphy and apomorphy. Phylogenetic analyses and Bayesian tip-dating including the reconstructed Yunxian 2 suggest that it is an early member of the Asian 'Dragon Man' lineage, which probably includes the Denisovans, and is the sister group of the *Homo sapiens* lineage. Both the *H. sapiens* and Dragon Man lineages had deep roots extending beyond the Middle Pleistocene, and the basal position of the Yunxian fossil cranium suggests it represents a population lying close to the last common ancestor of the two lineages.

One-Sentence Summary: The newly-reconstructed Yunxian 2 cranium represents a basal member of the Dragon Man and Denisovan lineage, and probably lies close to the last common ancestor of that lineage and the lineage of *H. sapiens*.

Main Text: Middle Pleistocene (Chibanian) human fossils show high morphological diversity. Some of those discovered recently, such as from Callao Cave in the Philippines, Rising Star Cave in South Africa, and Harbin in China, are so distinctly different from other fossil humans that they have been proposed as new species (*1-3*), additional to previously known taxa such as *H. sapiens*, *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, and *H. habilis*. It remains a matter of intense debate whether these morphologically diverse archaic humans represent multiple evolutionary lineages, or whether some are transitional variants leading to *H. sapiens*. Middle Pleistocene human fossils from China, sometimes called "archaic *Homo sapiens*," have been at the center of fierce debates about their relationship to *H. sapiens* over many years. Because of their even greater antiquity (*4, 5*) and apparent possession of both primitive features of *H. erectus* and arguably derived features of *H. sapiens* (*6, 7*), the two fossil crania from Yunxian, China (Yunxian 1 and 2) are crucial for interpreting the Middle Pleistocene record in China and reconstructing the evolution of *Homo* more generally. The best-preserved of the two crania, Yunxian 2, is nevertheless distorted, which has hampered attempts to infer its phylogenetic position. Here we reconstructed Yunxian 2, also using elements from Yunxian 1, and investigated its phylogenetic position. Given its geological age of 0.94-1.10 Ma (*5*) and the presence of mosaic features of plesiomorphy and apomorphy, Yunxian 2 probably lies close to the last common ancestor of *H. sapiens* and the Dragon Man lineage, and can also elucidate the evolutionary history of the Denisovans.

Our understanding of human evolution is largely based on fossil cranial specimens, but many fossils are incompletely preserved and/or distorted. Proper reconstruction of these imperfect fossils is therefore critical to studying their phylogenetic relationships. Reconstructions of *Sahelanthropus*, *Ardipithecus*, and *Homo habilis*, for example, have provided essential evidence regarding the early stages of human evolution (*8-11*). The Yunxian human fossils were discovered at a site on a terrace of the Hanjiang River in Yunxian County, Hubei Province, in central China. The site has yielded three crania so far (including a recently discovered and still unprepared cranium). Two previously known Yunxian crania, Yunxian 1 and 2, are both distorted. Yunxian 1 is crushed, with obvious plastic deformation. The distortion of Yunxian 2 is much less severe, and evaluation of high resolution CT scans indicates that the primary distortion is due to fragmentation and displacement rather than plastic deformation (Supplementary Materials). In a previous study, this cranium was virtually reconstructed mainly through keystone and symmetry corrections (*12*). The new reconstruction reported here is based on the least distorted cranium Yunxian 2, but also uses some data from Yunxian 1. The CT scans showed that the distortion of Yunxian 2 consisted mainly of small fractures and displacement of large fragments. We used methods developed in recent years (*8-11*), including virtual segmentation, separation and repositioning of the fragments, to correct the distortion.

As reconstructed, the Yunxian 2 cranium is large and long, with a platycephalic braincase in lateral view. It is smaller than the Harbin cranium (*H. longi*) and Xuchang, about the same size as Kabwe, Jinniushan, Petralona and Bodo, and larger than Sangiran 17 (*H. erectus*), Irhoud 1 and Maba specimens in overall dimensions. After reconstruction, the fossil lacks only small parts of the zygomaticarches and the missing central incisors.

The cranium is clearly plesiomorphic in overall form, with a broad supraorbital torus, basicranium and palate, a long and low vault in lateral view, and with a receding frontal and rather flat parietal contour. However, it lacks both the strongly angled occipital with a prominent transverse torus found in *H. erectus*, and *H. heidelbergensis/rhodesiensis* crania, and the protruding occipital region (occipital bun) with a central suprainiac fossa typical of *H.*

neanderthalensis. In posterior view, the slightly keeled cranium is widest in the supramastoid region, below which the large mastoid processes slope inward. In posterior view, the temporals and parietals converge superiorly, although not as strongly as in *H. erectus* fossils, and there is neither the upper parietal expansion found in recent *H. sapiens,* nor the "en bombe" shape typical of *H. neanderthalensis*. n lateral view the face is high and projects anteriorly as in *H. erectus,* and *H. heidelbergensis/rhodesiensis* fossils, but to a slightly lower degree. The nasal bones also project strongly anteriorly, but the midface is not pulled forwards as in *H. neanderthalensis*. The upper face and nasal aperture are wide. The zygomaxillary region is transversely flat and faces anteriorly, more comparable to the condition in European *H. antecessor* and the Asian *H. longi*, Dali, Jinniushan and Hualongdong fossils, as well as in *H. sapiens.* However, the cheek bones are large and high.

The matrix enclosed in the endocranial cavity of Yunxian 2 is very dense and the bone-matrix contrast of the CT scan is low. As a result, anatomical details such as the cranial vessel impressions on the inner surface of the cranial bones of Yunxian 2 cannot yet be reconstructed. Nevertheless, by setting 28 landmarks and measuring bone thickness, we were able to reconstruct the gross endocranial impressions and show that Yunxian 2 has a moderate endocranial capacity of about 1143 cc, similar to Dali, Hualongdong, Arago 21, Petralona and Ceprano. Its frontal lobe is low and narrow, barely more expanded than those of *H. erectus*, and *H. heidelbergensis/rhodesiensis*, and significantly less expanded than those of *H. neanderthalensis* (including the Sima de los Huesos fossils (*13*)) and *H. sapiens*. The posterior part of the parietal and occipital lobes are laterally and posteriorly expanded to a degree similar to *H. rhodesiensis*, Petralona, Dali, Jinniushan, Xuchang, and *H. neanderthalensis*. The dorsal expansion of the parietal lobe of Yunxian 2 is much less than that of *H. neanderthalensis* and *H. sapiens*.

Overall, the Yunxian cranium shows a distinctive combination of traits, and probably represents an additional species of *Homo* from other designated human taxa such as *H. erectus*, *H. sapiens*, *H. neanderthalensis*, *H. heidelbergensis/rhodesiensis*, *H. antecessor* and *H. longi*. The reconstructed Yunxian 2 provides new anatomical details for systematic comparison, inferring phylogenetic position, and testing phylogenetic models for the genus *Homo* in general. Our phylogenetic analyses were based on an updated data matrix containing 61 *Homo* OTUs and 649 discrete and continuous characters. We added *H. naledi*, *H. floresiensis*, Penghu, Xujiayao, Denisovans, and Yunxian 2. However, the Denisova Cave site so far contains only fragmentary human fossils, and only 19 (out of 649) characters could be scored. To assess the robustness of the phylogenetic inferences based on our restoration and reconstruction, we used the bootstrap method to resample the metric character scoring of Yunxian 2 (see details in Supplementary Materials). The results suggest that potential errors in our metric scoring have very little influence on the phylogenetic inferences we have made.

Parsimony analysis and Bayesian inference show that *H. sapiens*, *H. neanderthalensis*, Asian *H. erectus* and those Middle Pleistocene hominins traditionally referred to *H. heidelbergensis* (including Bodo and Kabwe) are all monophyletic groups. Most Asian Middle Pleistocene hominins, often previously referred to as "archaic *Homo sapiens*" including Dali, Jinniushan, Xujiayao, Hualongdong, group together with the Xiahe and Penghu mandibles to form a monophyletic group. These Asian Middle Pleistocene hominins are joined by the European *H. antecessor*. Together they form the sister group of a monophyletic *H. sapiens* clade. Here we call this whole sister group of *H. sapiens* the Dragon Man lineage, because *H. longi* is within this monophyletic group, although it forms a smaller monophyletic group with Yunxian and Dali.

Yunxian has the oldest age within the Dragon Man lineage, but is not the most basal fossil in our phylogenetic analyses.

Denisovan Cave in the Altai Mountains has yielded fragmentary fossil humans that are genetically identified as representing a distinct lineage from those of *H. sapiens* and *H. neanderthalensis* (*14, 15*). Analyses of mitochondrial DNA place Denisovans with the Sima de los Huesos fossils, and outside the divergence between *H. sapiens* and *H. neanderthalensis* (*16-18*), while nuclear genome sequences suggest that Denisovans are a sister group to *H. neanderthalensis* (*18, 19*). With only 3 lineages (*H. sapiens*, *H. neanderthalensis* and Denisovans), both possible phylogenetic relationships as reflected in the form of a tree topology are equally rational and logical, and depend on the choice of the rooting point of the tree, and it is also possible that analyses of separately inherited mitochondrial and autosomal DNA will give different results. Our parsimony analysis, based on the limited number of informative characters scored for the Denisovans, suggests that they belong to the Dragon Man lineage, but their exact position in the strict consensus tree cannot be determined. In the consensus tree generated by Bayesian inference, Denisovans are grouped with the Xiahe mandible, which in turn has been linked with Denisovans through a small amount of proteomic data (*20*). Known fossils of Denisovans are very fragmentary, and they have no parts in common with Xiahe. The grouping of Denisovans and Xiahe by Bayesian inference can be understood to mean that there is no other position that fits Denisovans better statistically than the grouping with Xiahe.

The topology of the *H. sapiens* group is identical to that in our previous phylogenetic model (*21*). Among the currently available early *H. sapiens* fossils, Irhoud 1 and 3 are the most basal fossils, consistent with previous arguments (*22*). The phylogenetic position of Florisbad remains debatable and its relationship to later humans is uncertain (*23, 24*). In our analyses, Florisbad falls in the monophyletic *H. sapiens* group, together with two other putative early *H. sapiens* from Africa (Laetoli Hominid 18 (*25*) and Omo 2 (*26, 27*)). These African early *H. sapiens* are paraphyletically related to the later appearing Eurasian *H. sapiens* fossils. With the exception of the Tabun C2 mandible, other Eurasian *H. sapiens* form a monophyletic group, with the western Asian Skhul 5 fossil as the most basal *H. sapiens* outside of Africa in our analysis.

European and West Asian *H. neanderthalensis* form a well-defined monophyletic group. The Sima de los Huesos humans had been suggested to represent *H. heidelbergensis* (*28*), but our analyses indicate that this is the most basal fossil within the *H. neanderthalensis* monophyletic group. The result is consistent with aDNA analyses and some recent morphological comparisons (*16, 28, 29*). Xuchang was paraphyletically related to the *H. neanderthalensis* group in our previous phylogenetic model (*21*). Here we found that Xuchang joins the *H. neanderthalensis* monophyletic group as the earliest divergent branch. Morphological comparisons have revealed that Xuchang shares some distinctive Neanderthal features, such as the presence of a suprainiac fossa, large endocranial volume, and small and medially inverted mastoid process (*30*). Unless these are a reflection of gene flow from Neanderthals, our analyses place Xuchang with the *H. neanderthalensis* monophyletic group as the earliest divergent branch.

Our updated phylogenetic analyses also shed light on the phylogenetic relationships of African and Asian *H. erectus*, African and European *H. heidelbergensis/rhodesiensis* and similar hominins, and the phylogenetic position of enigmatic fossil humans like *H. floresiensis* and *H. naledi*. The Asian *H. erectus* form a monophyletic group, but the African *H. erectus* fossils are paraphyletically related to each other and to the Asian *H. erectus*. African and European *H. heidelbergensis/rhodesiensis*, and similar fossils form a monophyletic group, unlike our previous analyses in which they form a paraphyletic group. *H. floresiensis* is the sister clade to Narmada,

and both taxa form the sister clade of Asian *H. erectus*. Such a result supports a previous hypothesis that *H. floresiensis* arose from a dwarfed population of early Asian *H. erectus* in an insular environment (*31-33*). *H. naledi* shows both primitive and derived features, and its phylogenetic position is still uncertain. In our analysis, *H. naledi* belongs to a distinct clade nested between African and Asian *H. erectus*.

The monophyletic group of the Dragon Man lineage shared 36 synapomorphies (S-Table 3), including characters such as broader frontal breadth, relatively broader anterior part of palate, lower inferior zygomatic margin height, lower mandibular corpus, relatively broader supraorbital torus, larger teeth, upper M3 reduction etc. As the sister of this group, the monophyletic lineage of *H. sapiens* shares 69 synapomorphies (S-Table 4), covering features such as narrower cranial vault, relatively broader biparietal breadth, shorter maxillary alveolar length, less projecting maxilla, higher vertical ramus of mandibula, deeper mandibular corpus, less midfacial prognathism, shallow glabellar inflexion, higher zygomaticoalveolar crest, thinner tympanic plate, presence of mental fossa etc. The monophyly of the Dragon Man and *H. sapiens* lineages is also well supported. The synapomorphies of this larger group include 18 characters, such as longer foramen magnum, broader frontal, longer basioccipital region, shorter parietomastoid suture, relatively narrower cranial vault, relatively broader frontal, presence of maxillary flexion, coronally oriented infraorbital plate, and gracile phalanx without ungual tuberosity expansion.

The Denisovans are known from very few specimens. When included in the phylogenetic analyses, the synapomorphies shared with other fossil humans of the Dragon Man lineage and shown in the preserved specimens include reduction of the M3, reduction of the metacone of the Upper M3, strengthening the Carabelli's cusp of M2, reduction of the M2 width, increases of M2 hypocone and cusp 5, and development of M3 crista obliqua. Morphological study of the Denisovan phalanx indicated that its dimensions and shape are within the range of *H. sapiens* (*34*). Presenting a gracile phalanx without expansion of the ungual tuberosity would thus be a shared derived feature of the Dragon Man lineage and *H. sapiens*.

Previous estimates of the divergence time between *H. neanderthalensis* and *H. sapiens* are about 0.5-0.7 Ma (*24, 29, 35*). However, a recent study based on the tree sequence of a large number of ancient genomes with 3589 samples to constrain the dating relationships revealed a much deeper ancestry in *H. sapiens* (*36*). The oldest ancestral haplotypes are about 2 Ma and geographically located in Africa. Our Bayesian tip-dating analysis also revealed that the diversification of *Homo* and the origin of *H. sapiens* have much greater time depths. The origin of the Dragon Man lineage can be inferred to be about 1.13 Ma, probably slightly older than the Yunxian fossils. The origin of the *H. sapiens* lineage is estimated to be about 0.93 Ma, also close to the age of Yunxian. The divergence between the Dragon Man lineage and the *H. sapiens* lineage is about 1.16 Ma. The monophyletic *H. neanderthalensis* lineage, widely thought to be sister to *H. sapiens*, diverged from the Dragon Man and *H. sapiens* lineages at about 1.27 Ma.

Given its geological age of 0.94-1.10 Ma (*5*), Yunxian is close to the theoretical origin time of the lineages of Dragon Man and *H. sapiens*. Our reconstruction of Yunxian 2 shows that this fossil human has mosaic features of plesiomorphies, as seen in *H. erectus*, and apomorphies, as seen in Dragon Man and *H. sapiens*. It is reasonable to conclude that Yunxian is morphologically and chronologically close to the last common ancestor of the lineages of *H. sapiens* and Dragon Man.

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Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S15

Tables S1 to S4

References (*1–109*)

Appendix 1-8

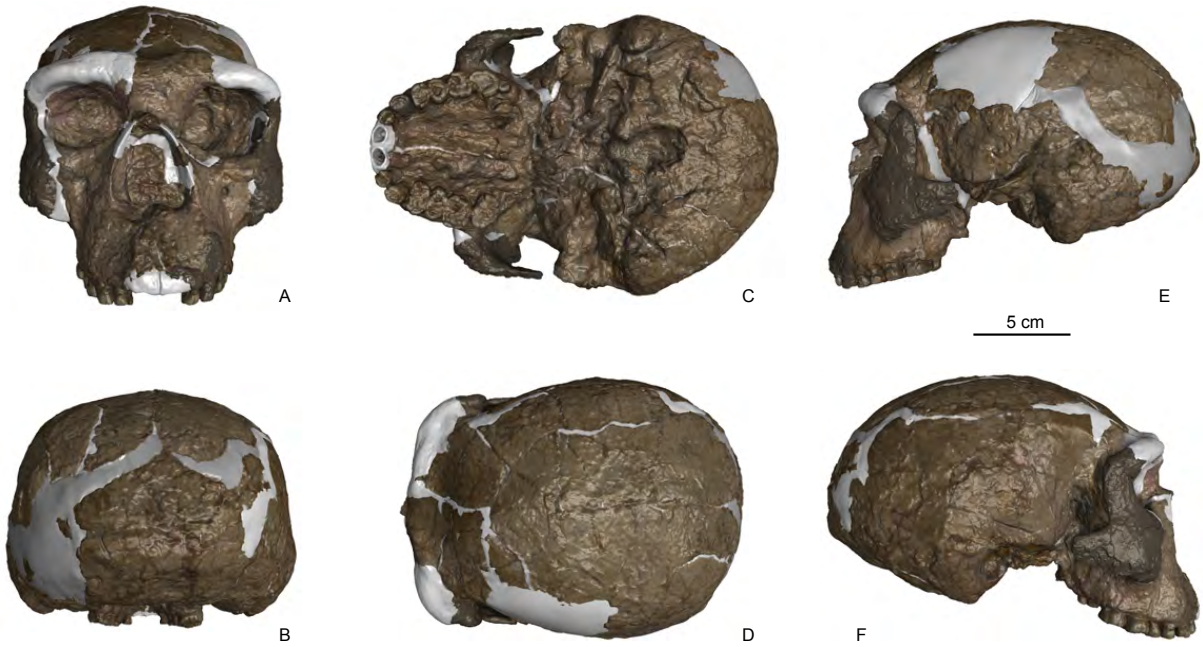

Fig. 1. Reconstruction of the Yunxian 2 cranium in standard views. (**A-F**) Anterior, posterior, inferior, superior, left and right views. Brown color indicates the fossil bone. White color indicates the reconstructed parts. Light grey indicates the bones crushed and covered by other bones and matrix. Scale bar indicates 5 cm.

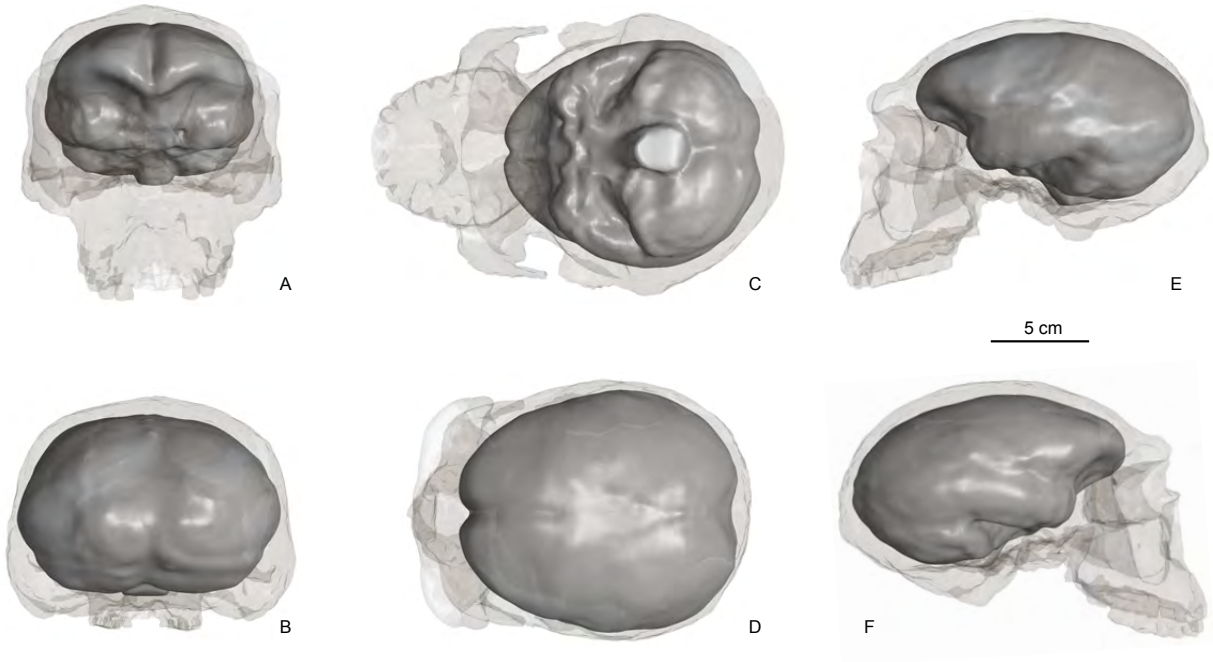

Fig. 2. Reconstruction of the endocranial cast of Yunxian 2. (**A-F**) Anterior, posterior, inferior, superior, left and right views. Scale bar indicates 5 cm.

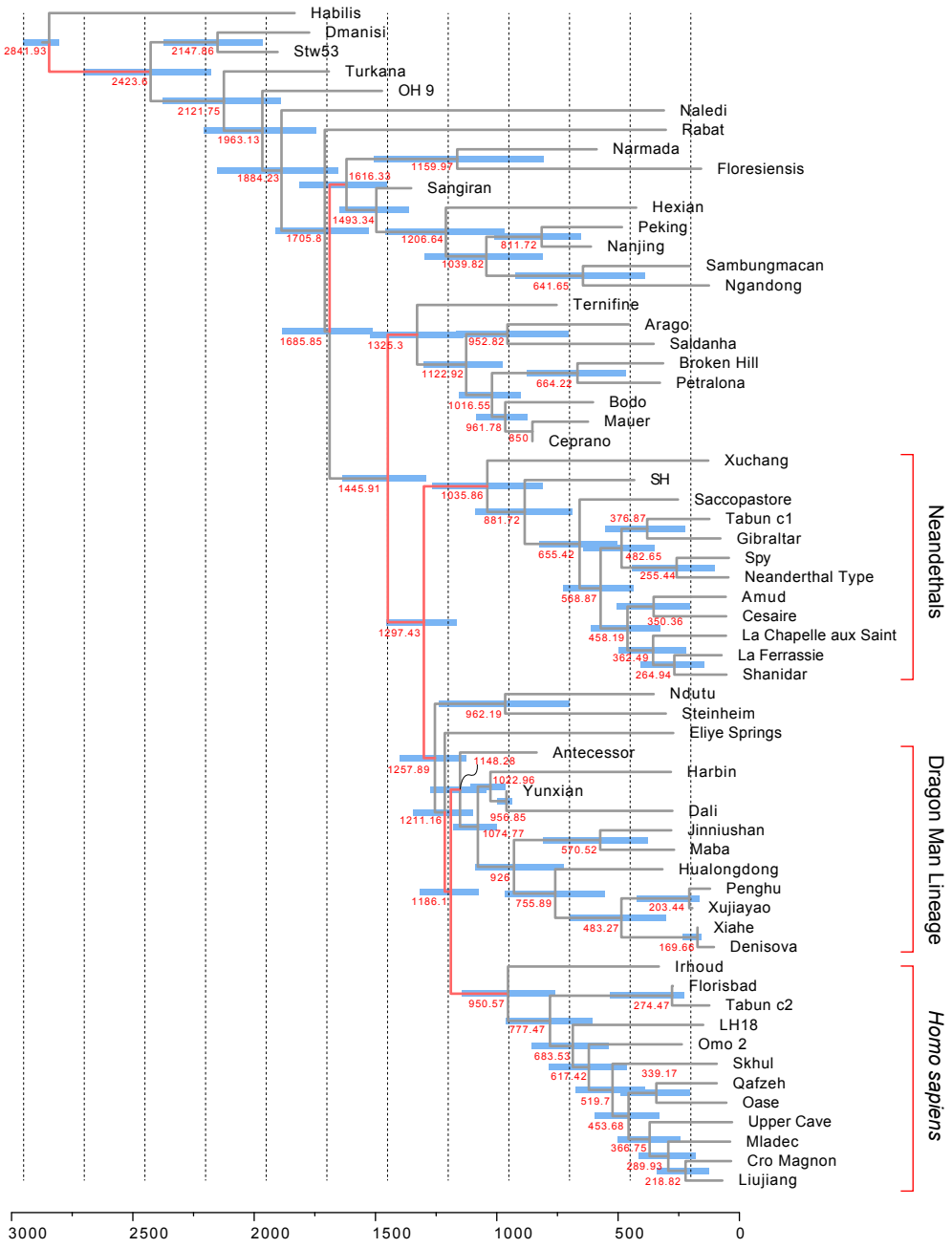

Fig. 3. Phylogeny of the 61selected fossil OTUs from the genus *Homo*. The topology of the tree was inferred from a Bayesian tip-dating analysis in MrBayes 3.2(*37*) and summarized as the all-compatible tree. To reduce the polytomy at some clades, the strict consensus of the most parsimonious trees from the parsimony analysis in TNT(*38*) was used as a reference. The branches in red indicate the backbone constraints based on the most parsimonious trees. Branch lengths are proportional to the division age in thousand years. Numbers at the internal nodes are the median ages, and the blue bars indicate the 95% highest posterior density interval of the node ages.